National University at Canberra. "It is an exciting time and in the next few years, a combination of these reconstruction methods with clever experiments and neurally realistic modelling will make huge advances in our understanding of navigational mechanisms and neuro-computational implementations." The advantage of insects, as Zeil points out, is that one can manipulate their natural behaviour within their natural environment in ways that wouldn't be possible with mammals or birds.

In a recent review of visual homing in insects (Curr. Opin. Neurobiol. (2012) *22*, 285–293), Zeil also mentions a few of the open questions in the field, including whether or not visual orientation requires the recognition of discrete objects, as opposed to more general panoramic impressions.

"In many experiments, indoors and out, insects clearly respond to individual objects. However, it is not clear what constitutes salient objects under complex natural conditions, because this will depend on both their salience in terms of the signals they provide against a noisy background and on the way information is extracted by the visual system of animals," Zeil explains. "We know that both localization of goals and direction of heading along routes can be achieved without segmentation of the visual scene into discrete objects, which is considered to be computationally demanding — but who knows?"

The biggest challenge is to find out how the insects store complex geographical information in their very small brains. "There are wonderful anatomical studies showing that certain parts of the brain of insects reconfigure themselves when exposed to information related to navigation," says Zeil. For instance, recent research demonstrates that the neuroanatomy of ants changes when they are exposed to light for the first time in their life (Dev. Neurobiol. (2010) *70*, 408–423). "So the question is," concludes Zeil, "will we be able to exactly map the available visual and motor-state information to the topography of these changes in the brain?"

Where do we go now?

Another important question is: what are you going to do if you're driving and the SatNav says one thing, your memory of the last trip says something else, and the person in the passenger seat has a different opinion altogether? We may have more or less rational ways of evaluating and combining information from different sources, but how do ants manage that?

This question, again, calls for mischievous manipulations, by which researchers can create conflicts between the separate navigation systems and can then observe how the problems are resolved, as Matthew Collett from the University of Exeter has recently reported in this journal (Curr. Biol. (2012) *22*, 927–932). His observations show that ants can use visual memory and path integration at the same time and may steer in a compromise direction if the two systems give conflicting results. Modelling shows that the observed behaviours can be explained by simple superposition of the outputs of the separate systems. "Insects show how much can be done with a relatively small brain and, through their limitations, suggest which processes really do require larger brains," Collett concludes.

Insect navigation is important for a whole range of reasons. For neuroscience, it offers the chance to observe information processing in manageable systems under conditions that are close to nature and thus relevant to evolutionary considerations. The crucial importance of navigation and homing behaviours is evident from the observation that most animals need these abilities to some extent — even sessile animals often have navigating larval stages.

Therefore it is no big surprise that evolution has driven natural navigation systems to a degree of perfection that human engineers can only dream of. "I think that every animal we look at is a more competent, more robust, more flexible, more miniaturized and a more energy-, material-, sensor- and computation-efficient agent than anything we have ever built," concludes Zeil. "So would anyone need more justification for how fundamentally important, intellectually challenging and promising it is to conduct research into the navigational abilities of insects?"

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Q & A

Tomoko Ohta

Tomoko Ohta, born in 1933, entered the Agriculture Department of the University of Tokyo, and after graduating in 1956, she worked at the Kihara Biological Institute. In 1962, she entered the PhD program at North Carolina State University. She received her PhD in 1966, and started her research career in 1967 at the Department of Population Genetics at the National Institute of Genetics, where Motoo Kimura was the head. In 1973, she presented her first major paper entitled 'Slightly deleterious mutant substitutions in evolution'. This theory was an expansion of Kimura's 'neutral theory', which Ohta called the 'nearly neutral theory' of molecular evolution. Her theory emphasizes the importance of interaction of drift and weak selection, and hence the role of slightly deleterious mutations in molecular evolution. With the accumulation of genome data, some of the predictions of the nearly neutral theory have been verified. The theory also provides a mechanism for the evolution of complex systems. Her other subject is to clarify the mechanisms of evolution and variation of multigene families. She has received several honors, including the foreign membership of the National Academy of Sciences, USA and Person of Cultural Merit, Japan.

What turned you on to biology and to your particular field of study?

After the Second World War, Japan was extremely poor, and children were encouraged to work and help their parents, rather than study. For me, as a high school student in 1950s Japan, the fortunate thing was that coeducation had just begun — up until then, girls could not enter good universities and my generation was the first in which female students were allowed. The atmosphere around me was such that girls were encouraged to have higher education. At high school, I liked mathematics, but was aware that it was difficult to find jobs in mathematics. People around me told that I should try going to

medical school. However, I failed the entrance exam, and instead entered the agricultural school of the University of Tokyo. Agronomy at that time did not interest me and I was truly at a loss about what to do after I graduated. After spending a few years at an editorial job at a publishing company, I was lucky enough to be hired at the Kihara Institute for Biological Sciences, Yokohama. There I worked on the cytogenetics of wheat and sugar beet. I was not terribly excited by cytogenetics at that time, and so I was glad to go abroad for more study, an opportunity provided by Hitoshi Kihara. Thus, I became a student at the Graduate School of North Carolina State University, in the US. There, I found the graduate courses in genetics and statistics very interesting, and I hoped to move from plant cytogenetics to population genetics. Ken-Ichi Kojima at the Genetics Department helped me to change my research field, and so I finally became his student, working on a problem in stochastic population genetics.

But, you chose not to stay in the US? I was a Fulbright student, and four years was the maximum time students were allowed to stay in the US. So, in 1966, after finishing my PhD, I went back to Japan. I asked Dr Motoo Kimura at the National Institute of Genetics, Mishima, if I could do research in his laboratory, simply because he was the only theoretical population geneticist in Japan at that time. At first, he was skeptical to let me do research in his field, but he finally accepted me as a postdoctoral fellow. Kimura was a typical Japanese man of his time, who regarded women's scientific activities as insignificant. After two years or so, I had convinced him that I should continue to do research.

And what were you working on? At that time, Kimura was thinking of combining the theory of stochastic population genetics, the field he had been working on, with biochemical data on the nature of the genetic material. He proposed his now famous 'neutral theory of molecular evolution' in 1968. The 'neutral theory' proposed that most evolutionary changes at the molecular level were caused by random genetic drift rather than by natural selection. Note that the neutral theory classifies new mutations as deleterious, neutral, and advantageous. Under this classification, the rate of mutant substitutions in evolution can be formulated by the stochastic theory of population genetics. Kimura's theory was simple and elegant, yet I was not quite satisfied with it, because I thought that natural selection was not as simple as the mutant classification the neutral theory indicated, and that there would be border-line mutations with very small effects between the classes. I thus went ahead and proposed the nearly neutral theory of molecular evolution in 1973. The theory was not simple, and much more complicated, but to me, more realistic, and I have been working on this problem ever since.

What has become of the 'nearly neutral' theory? Because of the emphasis on slightly deleterious mutations, the nearly neutral theory met strong objection in the 1970s and 1980s. For protein evolution, however, supporting evidence had begun to accumulate in the 1990s, and in this century, more such data have been gathered from genome analyses. Now, a most interesting problem is the relationship between near-neutrality and gene regulatory systems.

If you knew than what you know now, would you still pursue the same path? Yes I would. I like my professional field. I have been lucky to work in the Kimura laboratory. Although he was a typical Japanese man in daily life, he was quite liberal when it came to doing research, taking young people's ideas seriously. At that time, this was an unusual situation in Japanese laboratories.

How has modern genomics impacted your field of molecular evolution? Genomics provides large amounts of data. So, the testing of theories has become much more reliable. Also, the system-level approach has been made possible by genomics; that means people studying evolution and population genetics are now able to expand

their perspective by using genome data.

What is your greatest ambition? The current orthodox theory in evolution is Neo-Darwinism, which is based on Mendelian genetics. However, recent progress in developmental biology, and especially in uncovering epigenetic mechanisms, tells us that Mendelian genetics is not enough for describing certain phenomena of inheritance. Also, genomics is expanding rapidly such that analyses at the genomic level are needed for understanding evolutionary processes. My ambition is to combine these new findings with the nearly neutral theory in which the interplay of drift and weak selection is thought to be most important.

What do you think are the big questions in your field? If you look at systems biology papers, you are struck by extreme complexities of various interaction systems. To me, the biggest question is how such complex systems could have evolved? Once, a Japanese immunologist, Dr Tomio Tada, called the immune system an "immune super-system". It now seems that super-systems exist at so many levels in the biological world. Shifting and modification of these systems are essential for their evolution and variation.

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